Pesticides and bees: ecological-economic modelling of bee populations on farmland

Article (Accepted Version)

Ellis, Ciaran, Hanley, Nick, Kleczkowski, Adam and Goulson, Dave (2017) Pesticides and bees: ecological-economic modelling of bee populations on farmland. Ecological Modelling, 360 (24). pp. 53-62. ISSN 0304-3800

Pesticides and Bees: ecological-economic modelling of bee populations on farmland.

Adam Kleczkowski[1], Ciaran Ellis[1], Nick Hanley[2], and David Goulson[3]

[1] Faculty of Natural Sciences, University of Stirling, Stirling, Scotland, United Kingdom

[2] Dept. of Geography and Sustainable Development, University of St Andrews, St Andrews, Scotland, United Kingdom

[3] School of Life Sciences, University of Sussex, Brighton, United Kingdom

Corresponding Author:

Adam Kleczkowski

University of Stirling, Stirling, FK9 4LA, Scotland, United Kingdom

Email address: ak@maths.stir.ac.uk

Revised version, April 2017.

Abstract

Production of insect-pollinated crops typically relies on both pesticide use and pollination, leading to a potential conflict between these two inputs. In this paper we combine ecological modelling with economic analysis to investigate the effects of pesticide use on wild and commercial bees, whilst allowing farmers to partly offset the negative effects of pesticides on bee populations by creating more on-farm bee habitat. Farmers have incentives to invest in creating wild bee habitat to increase pollination inputs due to the contribution this makes to yields. However, the optimal allocation of on-farm habitat strongly depends on the negative effects of pesticides, with a threshold-like behaviour at a critical level of the impairment. When this threshold is crossed, the population of wild bees becomes locally extinct and their availability to pollinate breaks down. We show that availability of commercial bees masks this decrease in pollination services which would otherwise incentivise farmers to conserve the wild pollinator population. If commercial bees are available, optimum profit may be achieved by providing no habitat at all for wild bees, and allowing them to go extinct..

Keywords: pollination, pesticides, wild bees, commercial bees, ecological-economic modelling.

1. Introduction

Globally, around three-quarters of food crops are at least partly dependent on insect pollination [1], and this share has been rising over the past 50 years [2]. Ensuring sufficient pollination of these crops will be challenging in the future, due to adverse pressures on the supply of pollination services. Wild insect pollinator populations are threatened by both habitat loss, declines in foraging resources [3,4] and agricultural intensification [5,6], leading to population declines [6,7]. For some crops, honeybees are used to supplement or substitute wild pollinators, along with other commercial pollinators such as factory-reared bumblebees [8], although the majority of insect pollination for most crops is currently delivered by wild pollinators [9,10].

However, whilst commercial pollinators can be substitutes for wild pollinators for many crops, [11,12], the use of commercial pollinators is not without risk. Honeybees have suffered losses in recent years due to the abandonment of hives (Colony Collapse Disorder), the impacts of the *Varroa* mite and associated diseases [13] and falling numbers of bee keepers in some countries [14]. If losses of honeybees occur over a wide area, there can be an impact on the supply of these insects for pollination services, which can lead to cost increases to farmers; for example, prices for honeybee hire for use on almond farms doubled between 2006 and 2008 in the US [15]. Given the risks associated with reliance on commercial pollination sources, maintaining viable wild pollinator populations is likely to be crucial for sustaining the production of insect-pollinated crops into the future [10,16]. Moreover, as we show in this paper, the availability of commercial bees can mask declines in wild pollinators past a local extinction threshold, threatening the supply of a wide set of valuable ecosystem services from wild pollinators [39].

One of the factors implicated in the decline of insect pollinators such as bees is the use of pesticides. There is growing evidence of negative effects of commonly used insecticides on population- determining traits such as foraging rates and navigation in bees, on the overall growth and performance of colonies, and on the pollination services that they provide [17–24]. Awareness of this evidence has led to the temporary banning of the use on flowering crops of a widely used group of insecticides – neonicotinoids – within the European Union, but other insecticides are still widely used. Farmers of insect pollinated crops therefore face a dilemma, as one input (pesticides) is potentially dangerous to another (pollinators). One option, not investigated here, is to switch production to organic principles, and use zero pesticides. However, in the majority of global agricultural systems, abstaining from the use of all pesticides is not usually possible without large sacrifices in yields. Farmers must either attempt to reduce the impact of pesticides on wild pollinators, or increase the use of commercial pollinators, which can be replenished year after year.

Wild pollinators require habitat either off-farm or within the farm area. Although pollinating insects can forage over large distances, in intensive agricultural landscapes there is a decay in visitation of flowers by pollinators with increasing distance from the nearest habitat patch [25,26]. To offset this, farmers can encourage wild bees to nest within foraging distance of crops by providing nesting habitat and providing alternative foraging resources on the farm for when the crop is not in flower [3]. The effect of such interventions has been found to be strongest in intensively farmed areas [27] but depends also on the spatial location of bee-friendly habitat [28,29]. Hence, local or field-scale management practices may offset the negative impacts of intensive monoculture agriculture on pollination services to some extent [30].

In this paper, we develop an ecological-economic model to investigate the relations between two agricultural inputs, pollination and pesticides, and two sources of pollination with different characteristics; commercial pollinators, which can be replaced at a cost, and wild pollinators, which rely on a population being sustained within the farm area. Dedicating some of the farm area to sustain wild pollinators (eg by cultivating wild flower strips) is assumed to be costly in terms of foregone profits from a larger cropping area [31]. The model is parameterised using farm management data for strawberries, a relatively wellstudied crop on which both wild and commercial bees are used. The neonicotinoid pesticide thiacloprid is also commonly used in strawberry farming to protect the crop from destructive pests such as capsid bugs. Our modelling framework is, however, generalizable to other cropping systems where conflict occurs between pesticides, crop area and the survival of wild bee populations. . Our model improves on previous modelling attempts which have looked at either habitat considerations [28,29] or pesticide impacts [32] in isolation. In contrast, we combine these factors co-determining pollinator populations in a realistically-parameterised model which includes both economic and ecological behaviours.

2. Methods: the ecological economic model.

The model has three main linked components: the dynamics of the wild bee population; the production function which links bee populations and pesticide use to output, and farmers' decisions over which inputs to employ, represented via a profit function. We consider a farm that produces a single crop; parameters are chosen to represent a typical soft-fruit production system [33,34]. The farm has an area A which is divided into a wild bee habitat conservation area, vA, and a cropping area $(1-v)A$, where v is the proportion assigned to the wild bee habitat (for modelling purpose we vary this between 0% and 70%). Honeybees and commercially reared bumblebees can both provide pollination services for fruit production. For simplicity we consider all commercial (non-wild) pollinators to have the characteristics of commercially reared bumblebees in terms of nest size and pollinating efficiency, and generate results for both a scenario where all pollinators are affected by pesticides, and a scenario where wild bees are affected but commercial bees are not. These choices correspond to extreme situations; in reality it is possible that commercial pollinators are affected, but to a lesser extent than wild bees, since efforts can be made to minimise chemical exposure to commercial nests such as shutting the bees inside the boxes before spraying, or only spraying before the placement of nest boxes. Wild nests, on the other hand, may be exposed to multiple sprays of insecticides. Although both wild and commercial bumblebee nests are vulnerable to disease, wild nests are more likely to have infestations of parasites at the time spraying occurs (commercial bee boxes *should* arrive at the farms free from disease and therefore only pick up infections and parasites from that point onwards), putting wild bees at increased risk of any interactive effects between parasites and pesticides [35]

For simplicity we are assuming that the farm is a closed system with regard to wild or commercial bees, so that bees are not coming in from surrounding non-farmed habitat or leaving the farm. In reality bees do move between farms, which may buffer some of the more extreme effects predicted by our models (such as local extinction), and also means that bee populations supported by the actions of one farmer may benefit their neighbours. However, we do not capture the value of this external benefit in the model. We also assume no transfer of pesticides from outside the farm.

Wild bee population

The dynamics of the wild bee population is described in terms of $N(t)$ – a number of nests in a given year, *t*. This evolves according to equation (1):

$$N(t) = \min\Big(R\big(N(t-1) - D(t-1)\big), K\Big) \qquad (1)$$

where $N(t-1)$ is the number of nests at the beginning of year *t*-1, $D(t-1)$ represents the number of nests that die during year *t*-1. $N(t-1) - D(t-1)$ represents the number of live nests at the end of year *t*-1 that will reproduce in the following year. R is the reproduction rate, i.e. the number of new nests that each reproducing nest produces in the following year. The carrying capacity, *K*, is calculated from the likely on-farm nesting densities of wild bumblebees, N_w, under the assumption that wild bees nest in the conservation area only, $K = N_w vA$. The simple, piecewise linear function, equation (1), captures the essential features of the nest dynamics – exponential growth for small numbers of nests, limited by a carrying capacity, *K*, for large numbers. We also considered alternative formulation of (1) with a logistic functional form; this produces very similar results, so they are not shown in this paper.

Not all bumblebee nests will produce queens in a given year, and the likelihood of reproduction will depend in part on nest size. Pesticides can indirectly impact the likelihood of a nest reproducing by impairing the performance of foragers or increasing worker mortality and thus decreasing a nests' ability to gather and process resources. These impacts can lead to increased colony failure, either through early colony death or by limiting the number of new queens produced [19,20,23]. Bryden et al. [32] suggested a model in which the probability of nest death was inversely proportional to the number of foragers adjusted for pesticide impairments. Here we use an equivalent deterministic model in which a proportion d_N of nests dies in year t-1 so that[1]:

$$D(t-1) = d_N \times N(t-1) \; . \qquad (2)$$

Although in principle d_N can depend on time, in this model we assume the constant probability of nest death following [32],

$$d_N = \frac{m}{j + b_w} \qquad (3)$$

where b_w is an effective number of foraging wild bees per nest, $b_w = F_w(1 - w_w)$ with F_w being an average number of wild foragers per nest and w_w the impairment factor due to pesticides. If no pesticides are used,

[1] We also consider a stochastic equivalent of model (1), with nest deaths given by a random variable binomially distributed (with the maximum number of $N(t)$ and probability given by d_N): results are qualitatively similar to the ones presented here for the deterministic model.

or if pesticides are used but do not affect bees, $w_w = 0$; otherwise $w_w > 0$, reflecting for example, the effects on the navigational ability of honeybees which reduces the number of foragers which successfully return to the nest [18,19]. μ and ϕ are parameters determining the response of bumblebee population to pesticide (see Table 1).

Equation (1) can thus be rewritten

$$N(t) = \begin{cases} R \times \left(1 - \dfrac{m}{j + F_w \times (1 - w_w)}\right) N(t) & \text{if smaller than } K, \\ K & \text{otherwise.} \end{cases} \tag{4}$$

The initial condition is assumed to be $N(t) = K$ for t=0. Under this assumption $N(t)$ will stay constant for t>0, as long as:

$$R \times \left(1 - \frac{m}{j + F_w \times (1 - w_w)}\right) \geq 1 \tag{5}$$

and will decline exponentially to zero otherwise. In the following we assume parameter values such that condition (5) is always satisfied if and only if $w_w = 0$, that is, if there is no impairment due to pesticides.

Pollination and yield.

The single crop is pollinated by foragers originating from both wild and commercial nests. The total effective number of foraging wild bees is given by $B_w(t) = F_w(1 - w_w)N(t)$, whereas for commercial bees the effective number of foragers is assumed to be constant through time but proportional to the crop area, $B_c = F_c(1 - w_c)N_c(1 - v)A$. Here, F_c is the average number of foragers per commercial nest, w_c is the impairment of commercial bees due to pesticide use, N_c is the number of commercial nests per ha, and $(1 - v)A$ *(1-v) A* is the area under the crop (here we assume that commercial nests will only be placed where the crop is located, not in the area set aside as on-farm wild bee habitat). As for wild bees, if no pesticides are used or are used but have no effect on commercial bees, then $w_c = 0$.

Both wild and commercial bees are assumed to forage across the whole farm, over both crop land and the conservation area. The resulting effective density of foraging pollinators is then given by:

$$B(t) = \frac{B_w(t) + B_c}{A} = \frac{F_w(1 - w_w)N(t) + F_c(1 - w_c)N_c(1 - v)A}{A} . \tag{6}$$

Production.

The total farm production of a given crop in year *t* is given by $Y(t) \times (1 - v)A$ where $Y(t)$ is the current yield (in tonnes per ha) which is assumed to be a step-wise linear function of $B(t)$. We assume that without pollinators there is a set but low proportion, $\alpha Y_{\max}$, of a maximum yield ($Y_{\max}$) that can be achieved. When pollination is fully supplied, the maximum yield is given by $\gamma Y_{\max}$ with γ being a maximum proportion of high quality crop [36]. For intermediate values of $B(t)$ the yield per area in year *t* is given by:

$$Y(t) = Y_{\max} \times \min(\gamma, \alpha + \beta B(t)) \tag{7}$$

where γ is the maximum proportion of good quality fruit in the case of "full" pollination, α is the proportion of good quality fruits without bees and β is the incremental effect of bee visitation. The maximum attainable yield, $Y_{\max}$, depends on pesticide use and efficiency; we choose a higher value of $Y_{\max}$, $Y_{\max.p}$, if pesticides are used, and a lower value, $Y_{\max.nop}$, if they are not. As is the case for equation (1), in the light of limited available evidence this simple function captures the key elements of the yield dependence on supply of pollination services: an initial proportionality to the availability of bees and a saturation point at which additional numbers of pollinators have no further effect.

Farm economics.

There are two components to the profit function, the income from the sale of the crop and various costs, thus:

$\Pi(t)$ = Profit = Income – Cost of commercial bees – Pesticide costs – other costs.

The crop is sold at price *p* and with commission c_m so that the income is given by:

$$\text{Income} = p \times (1 - c_m) \times Y(t) \times (1 - v)A \; . \tag{8}$$

Note that this implicitly accounts for opportunity costs associated with the crop considered here, as it includes ‘lost’ income due to diminished area under crop.

Total costs for each year are the sum of variable (yield dependent) costs and other costs which include the costs of wild flower seeds, pesticides and commercial bees. Harvesting and packaging costs are assumed to be variable and calculated per tonne. We divide the costs into three components. “Other costs” do not directly depend on the usage of commercial bees or pesticides, and are given by:

$$\text{Other costs} = C_h \times Y(t) \times (1 - v)A + C_a \times (1 - v)A + C_f \times A + C_s \times v \times A \tag{9}$$

where C_h is the cost per tonne (harvesting and packaging), C_a is the cost per crop area (planting, structures, fieldwork), C_f is the fixed cost per area incurred regardless of whether it is cropped on not (e.g. land lease costs), and C_s is the cost of maintaining the wild bee conservation area (mainly providing seed and opportunity costs other than growing the crop considered here). If commercial bees are used, there is an additional cost of buying commercial nests which is proportional to the number of commercial nests per ha and the area under crop,

$$\text{Cost of commercial bees} = C_c \times N_c \times (1 - v)A \ . \tag{10}$$

In strawberry production, the main commercial bees used are bumblebees, which are purchased as disposable nests (sometimes called colonies) which last for up to 8 weeks. In other systems, farmers may rent honeybee hives for the duration of crop flowering.

If pesticides are used, there is additional cost associated with their purchase, assumed to be proportional to the area under crop,

$$\text{Cost of pesticides} = C_p \times (1 - v)A \ . \tag{11}$$

Decision making.

Our focus is on the decision is the farmer makes over the proportion of on-farm wild bee habitat, *v*, which is driven by profit maximisation over an extended period of time. We consider two contrasting cases. For the main part of the paper we calculate the profit after a long period of time when the wild bee population has fully responded to the strategy implemented at *t*=0 (in practice we use 200 years), thus

$$\max_{0 \le v \le 1} \left(\lim_{t \to \infty} \Pi(t) \right) \ . \tag{12}$$

This approach reduces dependency on (arbitrary) initial conditions and is equivalent to taking a long-term average without inclusion of any discounting. As an alternative we also consider an extension in which the profit is again calculated over a long time period, but with exponential discounting, so that

$$\max_{0 \le v \le 1} \left(\sum_{t=0}^{\infty} e^{-dt} \Pi(t) \right) \tag{13}$$

where *d* is a discounting factor. Note that the choice of *v* is made at *t*=0 and not changed afterwards. We analyse how the optimal choice of *v* and the resulting profit vary as pesticides are used or not, whether they affect wild or commercial bees, and whether the farmer decides to use commercial bees.

Parameters.

Although our model is generic for a permanent cropping system, we calibrated it to soft fruit production in the UK [33,34]. The numerical values for parameters used are listed in Table 1. K is calculated from the likely on-farm nesting densities of wild bumblebees. Nest densities will depend on the landscape type; around 11 to 15 nests per ha were found in non-linear countryside in a large scale survey in UK habitats, with higher densities in gardens and around linear features [37]. While actual densities will vary between locations, we assume that densities of 15 nests per ha can be found in on-farm habitat and assume that no nesting can occur within the cropped area. We follow Bryden et al. [32] in describing the effect of pesticide impairments on the dynamics of wild nests (Table 1). Costs of seeds, pesticides and bumblebee boxes are taken from a farm survey of 25 soft-fruit farms in Scotland [34]. Other production costs and prices per ha are taken from farm management data from the Farm Management Pocketbook(2016), [33] , corresponding to raised-bed June-bearing strawberries.

3. Results

We first analyse the optimal levels of conservation area provision, in the absence of pesticide use and commercial bees. The effect of pesticide on wild bees in considered next and then provision of commercial bees is considered, with and without the negative impact of pesticides on their ability to pollinate. We use equation (12), i.e. the long-term profit maximisation problem without discounting; the extension, equation (13), is addressed below.

RESULT 1: When no commercial bees or pesticides are used, profits are negative without on-farm wild bee habitat, and peak at low-moderate levels of its provision. Allowing for pesticide use shifts the yield and therefore the profit upwards, but the peak remains in the same position if pesticides have no adverse impact on wild bees.

We first consider a case when pollination is provided by wild bees only. If pesticides are not used, or if they are used but do not impair the pollination ability of wild bees (so that the wild bee impairment $w_w = 0$

), then profits and the population of wild bees are stable over time (assuming that the initial number of nests is $N(0)=K$). Profits peak when the on-farm habitat proportion is between 10% and 20% (Fig. 1a) as they depend on revenues made from the crop area, balanced against the loss through providing wild bee habitat rather than growing crops on the remaining area. At low levels of on-farm habitat provision, yield is limited by pollination, Fig. 1b, as

$$\alpha + \beta\, B(t) < \gamma \Rightarrow\ Y(t) = Y_{\max} \times \left(\alpha + \beta F_w \left(1 - \omega_w\right) N_w\, v\right) \tag{14}$$

(where we used the fact that $B(t) = \dfrac{F_w\left(1-\omega_w\right) N(t)}{A} = F_w\left(1-\omega_w\right) N_w\, v$ with $N(t) = K = N_w\, vA$; see Fig. 1c). Combining equations (6), (8) and (9) we see that for low values of the proportion of farm area under the crop, *v*, the leading term in the profit function is of the form *v*(1-*v*), see the left hand side of Fig. 1a. When *v* reaches the critical level

$$v = \frac{\gamma - \alpha}{\beta F_w \left(1-\omega_w\right) N_w} \tag{15}$$

(i.e. when $\alpha + \beta B(t) = \gamma$) then yield becomes independent on the wild bee population, but total production and therefore profit decreases as the area under cropping decreases with increasing *v*, as in figures 1a and 1b.

Profits can be negative when there is no area of the farm used for wild bee habitat and yields are low due to pesticides not being used, Fig. 1a. When pesticides are used (still under assumption of no adverse effect on wild bees), the profit function is shifted upwards (thick line in Fig. 1a), but this does not change the dynamics of wild bee population over time (Fig. 1c) or the optimal allocation of on-farm habitat. We note that if the initial density of the wild bumblebee nests, $N(0)$ is lower than *K*, the time projection of $N(0)$

will increase towards *K*. Profits in this case will also increase but in the long term the behaviour is the same as that discussed above.

RESULT 2: When no commercial bees are used and wild bees are impacted by pesticides ($w_w > 0$*), profits are lower and peak profits occur at higher level of on-farm bee habitat, as compared to the case without the impact.*

If the pesticide-induced impairment in pollination by wild bees is relatively small (eg. $w_w = 0.3$), the wild bee population stays constant over time (assuming $N(0) = K$, or increases until $N(0) \simeq K$ if $N(0) < K$), Fig. 2a. As a result, the yield is also constant, as in figure 2c. The corresponding profits are lower and require a higher proportion of on-farm habitat to peak, see equation (15) and Fig. 3a, as more nests (and therefore more habitat) are required to make up for the impairment of foragers by pesticides. These results are summarised in Fig. 4. Thus, with an increasing impact of pesticides on wild bees, there is a gradual increase in the optimal value of *v*, as shown in figure 4a (compared to figure 3a). This is associated with the gradual decrease in the corresponding maximum profit, as shown in figures. 3a and 4b. Farmers can thus, to a degree, compensate for the adverse impact of pesticides on wild bees by increasing on-farm bee habitat.

Wild bee numbers respond gradually to changes in the impairment as long as:

$$w_w \leq 1 - \frac{1}{F_w}\left[\frac{mR}{R-1} - j\right]; \qquad (16)$$

When (16) is not satisfied, the behaviour of the population of wild bees switches from sustainability over long periods of time, $N(0) = K$, to decline over time, $N(0) \to 0$ with $t \to \infty$, Fig. 2b. As a result, there is not enough pollination potential and production declines; in our parameterisation this occurs for $w_w > 2/3 = 0.666...$, see figure 4. We choose $w_w = 0.67$ to illustrate this behaviour in Fig. 2b and d. The resulting profits are significantly lower than for $w_w < 0.666...$ (Figs. 2d and 4b). The optimal percentage of on-farm habitat changes in time and is initially ca. 50%, higher than when there is no impact of pesticides on wild bees.

The qualitative change in the long-term dynamics of wild pollinators results in a threshold-like behaviour for optimal proportion of on-farm habitat, *v*, Fig. 4a, and the associated maximum profit, Fig. 4b, both of which drop rapidly at the transition point, cf. equation (16). This points to very high sensitivity of the results to the effects of pesticides on wild bee population as the threshold of $w_w = 0.666...$ is approached.

RESULT 3: The speed at which wild bumblebees decline depends on the balance of nest death relative to nest reproduction.

When wild bees are used as the sole pollination input, the likelihood of wild bee decline depends on the relationship between the impairment of foragers (and hence nest survival) and the reproductive capacity of the surviving nests each year (Fig. 2b). If the impairment is high enough, the density of nests declines exponentially in time as

$$N(t) = N(0) \times \exp(-rt) \quad \text{with} \quad r = -\ln\left[R \times \left(1 - \frac{m}{j + F_w \times (1 - w_w)}\right)\right]. \quad (17)$$

Thus, the characteristic time for the decline, i.e. the time needed for the population to decline from $N(0)$ to $e^{-1}N(0)$, is given by r^{-1} and sharply decreases when w_w increases, Fig. 5, independently of *v*.

However, the resulting decline in the profit can initially be slow (see an example in Fig. 6), effectively masking the decline in nest density (to illustrate this effect better, N_w is increased by a factor of 5 so that the resulting K is higher in Fig. 6 than in other figures). With higher levels of on-farm habitat, there are more wild bees per area of crop, and so there is a period where farms are over supplied with pollinators (this may have negative consequences in some crops as it could lead to too many fruits produced, see e.g. [36]). This continues until the wild bee population drops to a level at which pollination services become limited, at which point profits begin to drop (Fig. 6). Thus, the farmer might not have an incentive to change the pesticide use until populations are too low to recover.

RESULT 4: When commercial bees are used (and unaffected by pesticides), profits remain stable despite declines in wild bees, and are highest when on-farm habitat is low

When commercial bees are used at the same time as wild bees, Fig. 3b and 4b, the highest profit corresponds to no on-farm habitat, i.e. v=0. The resulting optimal profit is higher than when pollination relies on wild bees only. The slight drop in the profit at higher values of v in Fig. 3b is due to the cost of buying in commercial bees.

Profits remain stable throughout the projection period regardless of whether wild bee nests decline or not, Figs. 3b, 4b and 7a, with highest yields when no farm area is set aside for habitat. Thus, when farmers can buy-in pollinators which are unaffected by pesticides, and where such commercial bees can provide a perfect substitute for wild bees in terms of their pollination delivery, this acts as a severe disincentive to conserving wild bees or to reduce pesticide use.

RESULT 5: When commercial bees are used and both these and wild bees are affected by pesticides, the optimal strategy is either to rely completely on commercial bees, or to provide a mixture of commercial bees and on-farm habitat for wild bees, depending on the level of impairment.

When both commercial and wild bees are impaired by pesticides, profits generally change little if the impairment is low and equation (16) is satisfied, as shown in figure 4. The optimal area of on-farm habitat is zero, so all pollination is provided by commercial bees. If the impairment is increased (but (16) is still satisfied) it becomes profitable to invest in a mixture of wild and commercial bees, as shown by the dash-dot line in Fig. 3b and the intermediate range of w_w and w_c in Fig. 4a (here we assume $w_c = w_w$). This is also associated with a drop in optimal profit as compared to the case when commercial bees are unaffected by pesticides, Fig. 4b. The wild bee population remains steady for low impairment levels (if (16) is satisfied) and starts to decline when impairment becomes too high, resulting in the return to pollination based on commercial bees only, see the drop in Fig. 4a. Profits continue to decline with increasing impairment, as the reduced number of commercial bee foragers cannot provide the entire pollination service, leaving crops vulnerable to pollinator decline (we assume that farmer does not change the provision of commercial bees over time: clearly, this assumption can be relaxed). However, the decline in profits at this point is smaller than if the commercial bees are not used, Fig. 4b, as the commercial bees still manage to moderate the adverse impacts of pesticides.

When the impairment is high and both commercial and wild bees are affected, profit declines over time unless v=0, Fig. 7b. Initially, when there is still sufficient number of wild bee nests, the optimal strategy is to invest in a mixture of wild and commercial bees, Fig. 7b. As wild bee nests die due to pesticide impairment, the farmer starts to rely on commercial bees only, even though they are also affected by pesticides.

RESULT 6: If the decision maker discounts the future benefits (i.e. follows equation (13) rather than (12)) in presence of current sufficient pollination supply by wild bees (i.e. $N(0) \simeq K$), there is a region of the impairment values for which it is optimal to continue investing in the on-farm habitat, even if in the long term wild bees can become locally extinct.

So far, we have assumed that the decision maker concentrates on the long-term outcome of the strategy, i.e. follows equation (12). Very similar result is obtained if instead the decision maker uses the total profit over time without discounting future costs and benefits, equation (13) with d=0; in this case the total profit is dominated by the long-term behaviour of $N(t)$ and consequently $Y(t)$. If d>0, then the outcome depends on the transient dynamics of $N(t)$. The optimal choice of v is in this case similar to the case with no discounting for a wide range of w_w, figure 8(a), except just above the local extinction threshold (16). If wild bees are initially present, $N(0) \simeq K$, it might take a long time until their population decays. Thus, rather than reducing their number outright by setting v=0 (as is the case for d=0), it is more profitable to allocate some area of the farm to temporarily keep the wild population even if it is declining due to pesticide effects. The danger of this solution is that in the long-term it still leads to the wild bee population extinct, even though it might take a long time (as discussed above), figure 8(b).

Discussion and Conclusions.

Pollination inputs are valued by farmers as they increase the quality and quantity of a range of important crops [38]. Using an ecological-economic model, we show that it can be rational for a farmer to allow wild bee populations on their land to decline, since this reflects a short-term trade-off with the benefits of increased pesticide use. Moreover, the availability of commercial bees as a substitute for wild bees can effectively mask declines in wild bees towards a local extinction threshold,, and reduces the private value of wild bee conservation on farms. Whilst not considered directly here, there may also be lags in the response of insect pollinators to pesticide use, meaning that the market signal to farmers to change their management practice arrives “too late” to stop a permanent decline in pollinators. Since wild pollinators also generate ecosystem benefits for a wide range of wild plants beyond the farm from which society derives value [39], these three factors can all drive the supply of wild bees below the social optimum.

In the modelling presented above, we consider the pollination services provided by a mix of wild and commercial bees which are inputs to a commercial crop. Farmers can “produce” more wild bees by allocating land to bee habitat, but this comes at an opportunity cost in terms of foregone profits from land allocated to cropping. Use of a third input, pesticides, contributes positively to profits through its effect on output, but negatively through any effects on bees. Farmers thus face a trade-off in the costs and benefits of pesticide use, where these costs go beyond the price paid for pesticides.

If commercial bees are unaffected by pesticides, their small cost relative to other inputs means that profits are highest when commercial bees are used and little farm area is converted to on-farm habitat for wild bees. If wild bee numbers decline under pesticide pressure, profits can remain positive, as commercial bee numbers can deliver the required pollination level for maximum yields. This is in contrast to the situation when wild bees alone are used for pollination and there is no option to use commercial bees. When only wild bees provide pollination, it is optimal for farmers to convert some of their crop land to wild bee habitat, a results which is in accordance with other studies [28,29]. How big an area of land is allocated to bee habitat will depend on crop prices and the productivity of land, both for wild bees and for crops.

The outcome changes when commercial bees are impaired by pesticides along with wild bees. In this case, agricultural yields can be stable and high for a number of years and then fall suddenly, as wild pollinators decline past a particular point. High yields are maintained when there is an “over-supply” of pollinators, but fall after wild pollinators numbers decline to a level where overall pollinator numbers limit yields.

In practice, the relative impact of pesticides on commercial and wild bees will depend on farm management practices. Farmers can reduce the impact on commercial bees by shutting the hives or nest boxes when spraying takes place, though systemic pesticides, by design, are likely to persist within the plant for weeks after application, so bees will still be equally exposed through the ingestion and transport of contaminated nectar and pollen [7]. Wild pollinators cannot be shut inside nests while spraying takes place and so are more vulnerable, though some action can still be taken to avoid direct impact on wild pollinators such as spraying when wild bees are not active.

If declines in wild pollinators are irreversible (e.g. as species become extinct), and if there is uncertainty over whether wild pollinators will be more beneficial in the future (e.g. as new crop varieties, more dependent on insect pollinators, are bred), then there is an option value to maintaining this natural capital for future use [40,41]. This option value is an additional economic rationale for conserving wild pollinators, even when there are commercial pollinators present. This value, however, will depend on the time-horizon and risk-aversion of the farmer, as farm profits may be stable for years before declines are evident. If farmers are present-bias, then there may be little private benefit to conserving wild pollinators for future crop production, implying that government interventions may be required given the wide range of economic and ecological benefits which wild pollinators deliver [39,42].

The wild bee population modelled here will often in practice be made up of multiple populations of bee and non-bee pollinators such as hover-flies, wasps and beetles [11]. The presence of multiple pollinator groups can buffer the system from extinction [43,44], and we have not modelled this buffering capacity here. While different pollinators groups may respond in different ways to external pressure such as pesticide use, the effects are likely to be negative on all groups, and may be stronger on solitary bees and non-bee pollinators as these are often smaller in size and they are not buffered by living in a social colony with numerous expendable workers [21,45]. There is a benefit from maintaining multiple groups of ecosystem service providers as insurance against a fluctuating environmental conditions [46], implying a role for commercial bees in providing "financial insurance" against wild bee declines. On the other hand, commercial bees may contribute to wild bee decline, e.g. by introducing or spreading disease.

Several simplifications made in the modelling procedure should be noted. We have assumed that all factors are deterministic. In reality key processes like pollination or be reproduction and death will be stochastic. We assumed that all nests which reproduce produce a set number of queens which survive until the next year, since this simplifies the actual process which will rely on perhaps a larger number of queens being produced by successful colonies, who then may or may not mate, survive until the next year and establish a nest themselves. Overall success is likely to depend on other factors such as weather conditions and the level of disturbance, so the failure rate will vary substantially between years [32]. There is evidence that pesticides can interact synergistically with diseases, poor nutrition and other chemicals, but this is not modelled either [22,35,47]. Moreover, if commercial bee keepers find that their bees are being adversely affected by pesticides, then supply may decline, leading to a future rise in the prices charged for commercial pollinator services.

Our model describes a static permanent crop system which is grown every year with no change to agricultural practices over time. While this might be suitable for crops like strawberries which are grown every year, in many arable systems rotation will affect the year-to-year demands for services and resources available for pollinators. We also ignore feedbacks between the changes to yield and therefore profit and farm management strategies. In reality, farmers may respond to the decrease in availability of pollination services by changing the density of commercial nests or lowering the use of pesticides. We also assume that prices and costs are constant over time and do not depend on the overall level of production.

We consider the bee population on the farm in isolation. Migration from outside will affect the rate at which the population changes over time; for example queens of wild bees are mobile so that farms with low or zero bee populations are likely to receive net immigration of nesting queens in spring. This may fill gaps in the resident population and protecting against local extinction, though the farm would then be acting as a sink, reducing the bee population on the surrounding farms. Similarly, foraging bees may fly several kilometres from their nest, spilling out from farms which have taken measures to provide habitat for them, and pollinating crops on neighbouring farms which have deployed no such measures. Discouraging such free riding may require financial incentives which reward those who act to increase the stock of wild pollinators at the landscape level, whoever benefits.

Our model also considers only two species, wild and commercial bees. In practice, different species will have different life patterns, different pollination ability, and will differ in their response to pesticides. The model presented here can be extended to multiple species, but will be even more difficult to parameterise. Moreover, if the two insect pollinator species considered were more variable in their tolerance of weather conditions than the two species considered (commercial and wild bumblebees). If the commercial bees were honey bees, then these are less tolerant of certain weather conditions than (wild) bumblebees. In that case, a portfolio approach to management of pollinator resources on a farm would be more in favour of maintaining a mix of wild and commercial bees as a way of managing risk [48].

We have based model parameters on a specific crop, strawberries. As Keitt [28] concluded, the actual form of the production relationship between pollinators and profits is likely to vary across and within crops, depending on the yield response to both pesticides and bees, and the landscape in which the farmers are working. However, our model is applicable for a range of crops with similar or higher dependency on bees which also benefit from applications of pesticides, and which are grown within intensive agricultural environments, including other soft-fruits and almonds.

We show that pesticide use is not only an externality, affecting wild bees in the vicinity of the farm, but part of an internal trade-off decision for farmers of insect pollination-dependent crops. In the presence of commercial bees, farmers have little incentive to support wild bees around their farms; while bees might be important to crop yields, the availability of cheap substitutes means that high profits can be maintained in the short-term. This is despite a longer term risk of declining profits which can threaten the ability of farmers to maintain production over time. Safeguarding farmland pollinators may therefore require monetary incentives to encourage the creation of on-farm habitat so that future pollination options are not reduced. The economic case for such incentives, funded by the taxpayer, is strengthened when one also considers the non-market benefits of wild pollinators, and the external benefits to neighbouring farmers.

References

1. Klein, A.-M., Brittain, C., Hendrix, S. D., Thorp, R., Williams, N. & Kremen, C. 2012 Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* **49**, 723–732. (doi:10.1111/j.1365-2664.2012.02144.x)

2. Aizen, M. A. & Harder, L. D. 2009 The Global Stock of Domesticated Honey Bees Is Growing Slower Than Agricultural Demand for Pollination. *Curr. Biol.* **19**, 915–918. (doi:10.1016/j.cub.2009.03.071)

3. Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D. & Nowakowski, M. 2007 Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* **44**, 29–40. (doi:10.1111/j.1365-2664.2006.01249.x)

4. Winfree, R. et al. 2009 Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. Biol. Sci.* **276**, 229–37. (doi:10.1098/rspb.2008.0709)

5. Biesmeijer, J. C. et al. 2006 Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science (80-.).* **313**, 351–354. (doi:10.1126/science.1127863)

6. Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F. & Griswold, T. L. 2011 Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci.* **108**, 662–667. (doi:10.1073/pnas.1014743108)

7. Goulson, D. et al. 2015 Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**, 1255957. (doi:10.1126/science.1255957)

8. Velthuis, H. H. W. & Van Doorn, A. 2006 A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie* **37**, 421–451. (doi:10.1051/apido)

9. Breeze, T. D., Bailey, A. P., Balcombe, K. G. & Potts, S. G. 2011 Pollination services in the UK: How important are honeybees? *Agric. Ecosyst. Environ.* **142**, 137–143. (doi:10.1016/j.agee.2011.03.020)

10. Garibaldi, L. A. et al. 2013 Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**, 1608–11. (doi:10.1126/science.1230200)

11. Brittain, C. et al. 2013 Synergistic effects of non-Apis bees and honey bees for pollination services. *Proc. Biol. Sci.* **280**, 20122767. (doi:10.1098/rspb.2012.2767)

12. Brittain, C., Kremen, C. & Klein, A.-M. 2013 Biodiversity buffers pollination from changes in environmental conditions. *Glob. Chang. Biol.* **19**, 540–547. (doi:10.1111/gcb.12043)

13. Cox-Foster, D. L. et al. 2007 A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* **318**, 283–7. (doi:10.1126/science.1146498)

14. Potts, S. G., Roberts, S. P. M., Dean, R., Marris, G., Brown, M. A., Jones, R., Neumann, P. & Settele, J. 2010 Declines of managed honey bees and beekeepers in Europe. *J. Apic. Res.* **49**, 15–22. (doi:10.3896/IBRA.1.49.1.02)

15. Pettis, J. S. & Delaplane, K. S. 2010 Coordinated responses to honey bee decline in the USA. *Apidologie* **41**, 256–263. (doi:10.1051/apido/2010013)

16. Winfree, R., Williams, N. M., Dushoff, J. & Kremen, C. 2007 Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* **10**, 1105–1113. (doi:10.1111/j.1461-0248.2007.01110.x)

17. Mommaerts, V., Reynders, S., Boulet, J., Besard, L., Sterk, G. & Smagghe, G. 2010 Risk assessment for side-effects of neonicotinoids against bumblebees with and without impairing foraging behavior. *Ecotoxicology* **19**, 207–215. (doi:10.1007/s10646-009-0406-2)

18. Henry, M. et al. 2012 A common pesticide decreases foraging success and survival in honey bees. *Science* **336**, 348–50. (doi:10.1126/science.1215039)

19. Gill, R. J., Ramos-Rodriguez, O. & Raine, N. E. 2012 Combined pesticide exposure severely affects individual- and colony-level traits in bees. *Nature* **491**, 105–108. (doi:10.1038/nature11585)

20. Whitehorn, P. R. et al. 2012 Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science* **336**, 351–2. (doi:10.1126/science.1215025)

21. Goulson, D. 2013 REVIEW: An overview of the environmental risks posed by neonicotinoid insecticides. *J. Appl. Ecol.* **50**, 977–987. (doi:10.1111/1365-2664.12111)

22. Goulson, D. 2015 Neonicotinoids impact bumblebee colony fitness in the field; a reanalysis of the UK's Food & Environment Research Agency 2012 experiment. *PeerJ* **3**, e854. (doi:10.7717/peerj.854)

23. Rundlöf, M. et al. 2015 Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature* **521**, 77–80. (doi:10.1038/nature14420)

24. Stanley, D. A., Garratt, M. P. D., Wickens, J. B., Wickens, V. J., Potts, S. G. & Raine, N. E. 2015 Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* **528**, 548–550. (doi:10.1038/nature16167)

25. Ricketts, T. H. et al. 2008 Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515. (doi:10.1111/j.1461-0248.2008.01157.x)

26. Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J. & Sanderson, R. A. 2008 Bumblebee flight distances in relation to the forage landscape. *J. Anim. Ecol.* **77**, 406–415. (doi:10.1111/j.1365-2656.2007.01333.x)

27. Carvell, C., Osborne, J. L., Bourke, A. F. G., Freeman, S. N., Pywell, R. F. & Heard, M. S. 2011 Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecol. Appl.* **21**, 1760–1771. (doi:10.1890/10-0677.1)

28. Keitt, T. H. 2009 Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol. Appl.* **19**, 1561–1573. (doi:10.1890/08-0117.1)

29. Brosi, B. J., Armsworth, P. R. & Daily, G. C. 2008 Optimal design of agricultural landscapes for pollination services. *Conserv. Lett.* **1**, 27–36. (doi:10.1111/j.1755-263X.2008.00004.x)

30. Kennedy, C. M. et al. 2013 A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* **16**, 584–599. (doi:10.1111/ele.12082)

31. Breeze, T. D., Bailey, A. P., Balcombe, K. G. & Potts, S. G. 2014 Costing conservation: an expert appraisal of the pollinator habitat benefits of England's entry level stewardship. *Biodivers. Conserv.* **23**, 1193–1214. (doi:10.1007/s10531-014-0660-3)

32. Bryden, J., Gill, R. J., Mitton, R. A. A., Raine, N. E. & Jansen, V. A. A. 2013 Chronic sublethal stress causes bee colony failure. *Ecol. Lett.* **16**, 1463–1469. (doi:10.1111/ele.12188)

33. Nix, J. 2015 *John Nix Farm Management Pocketbook 2016.* Agro Business Consultants Ltd.

34. Ellis, C. 2014 Valuing wild pollinators for sustainable crop production: PhD Thesis, University of Stirling.

35. Alaux, C. et al. 2010 Interactions between Nosema microspores and a neonicotinoid weaken honeybees (Apis mellifera). *Environ. Microbiol.* **12**, 774–782. (doi:10.1111/j.1462-2920.2009.02123.x)

36. Garratt, M. P. D., Breeze, T. D., Jenner, N., Polce, C., Biesmeijer, J. C. & Potts, S. G. 2014 Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agric. Ecosyst. Environ.* **184**, 34–40. (doi:10.1016/j.agee.2013.10.032)

37. Osborne, J. L., Martin, A. P., Shortall, C. R., Todd, A. D., Goulson, D., Knight, M. E., Hale, R. J. & Sanderson, R. A. 2007 Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *J. Appl. Ecol.* **45**, 784–792. (doi:10.1111/j.1365-2664.2007.01359.x)

38. Klatt, B. K. et al. 2014 Bee pollination improves crop quality, shelf life and commercial value. *Proc. Biol. Sci.* **281**, 20132440. (doi:10.1098/rspb.2013.2440)

39. Hanley, N., Breeze, T. D., Ellis, C. & Goulson, D. 2015 Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosyst. Serv.* **14**, 124–132. (doi:10.1016/j.ecoser.2014.09.013)

40. Arrow, K. J. & Fisher, A. C. 1974 Environmental Preservation, Uncertainty, and Irreversibility. In *Classic Papers in Natural Resource Economics*, pp. 76–84. London: Palgrave Macmillan UK. [cited 2016 Aug. 8]. (doi:10.1057/9780230523210_5)

41. Kassar, I. & Lasserre, P. 2004 Species preservation and biodiversity value: a real options approach. *J. Environ. Econ. Manage.* **48**, 857–879. (doi:10.1016/j.jeem.2003.11.005)

42. Hoehn, P. et al. 2008 Functional group diversity of bee pollinators increases crop yield. *Proc. Biol. Sci.* **275**, 2283–91. (doi:10.1098/rspb.2008.0405)

43. Memmott, J., Waser, N. M. & Price, M. V 2004 Tolerance of pollination networks to species extinctions. *Proc. Biol. Sci.* **271**, 2605–11. (doi:10.1098/rspb.2004.2909)

44. Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B. & Caflisch, A. 2010 The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* **13**, 442–452. (doi:10.1111/j.1461-0248.2009.01437.x)

45. Henry, M. et al. 2015 Reconciling laboratory and field assessments of neonicotinoid toxicity to honeybees. *Proc. Biol. Sci.* **282**, 806–807. (doi:10.1098/rspb.2015.2110)

46. Baumgärtner, S. 2007 The insurance value of biodiversity in the provision of ecosystem services. *Nat. Resour. Model.* **20**, 87–127. (doi:10.1111/j.1939-7445.2007.tb00202.x)

47. Laurino, D., Porporato, M. & Patetta, A. 2011 Toxicity of neonicotinoid insecticides to honey bees: laboratory tests. *Bull. Insectology* **64**, 107–113.

48. Convertino, M., & Valverde Jr, L. J. (2013). Portfolio decision analysis framework for value-focused ecosystem management. *PLoS One* 8(6), e65056.

Table 1: Key parameters in the model (modelled after soft fruit production).

Parameter	Interpretation	Value	Source/comments
v	Proportion in conservation area	0-0.7	Key variable
A	Farm area	100ha	Assumed
R	Nest reproduction ratio	4	Incorporates the relatively small chance of queens mating and overwintering
N_w	Wild bees nesting density	15	[37]
N_c	Commercial bees nesting density	4	[20] gives estimates of 0.32-8.75 imported boxes per ha per year
μ	Nest death parameter	55	[32]
ϕ	Nest death parameter	40	[32]
F_w	Avg. number of wild foragers per nest	100	[34]
F_c	Avg. number of commercial foragers per nest	100	Same as F_w
w_w	Impairment due to pesticides, wild bees	0 if no impairment; variable	Key variable
w_c	Impairment due to pesticides, commercial bees	0 if no impairment; variable	Key variable
$Y_{max.nop}$	Maximum attainable yield when pesticides are not used	11.5 tonne per ha	Estimated from [33] as 50% of max yield
$Y_{max.p}$	Maximum attainable yield when pesticides are used	23 tonne per ha	Max yield in [33]

γ	maximum proportion of good quality fruits	0.9	[34]
α	proportion of good quality fruits without bees	0.35	[34]
β	incremental effect of bee visitation	0.0024	Combined visitation and efficiency in [34]
p	Price per tonne	3445	[33]
c_m	Commission	0.09	[33]
C_h	Cost per tonne (harvesting and packaging)	£1650 per tonne	[33]
C_a	Cost per crop area (planting structures, fieldwork)	£18700 per ha	[33]
C_f	Fixed cost per area (land lease)	£150 per ha	[33]
C_s	Cost of maintaining the conservation area (mainly seed)	£100 per ha	[33]
C_c	Cost of commercial nests, per nest	£60 per nest	[33]
C_p	Cost of pesticide use, per ha of crop area	£10 per ha	[33]

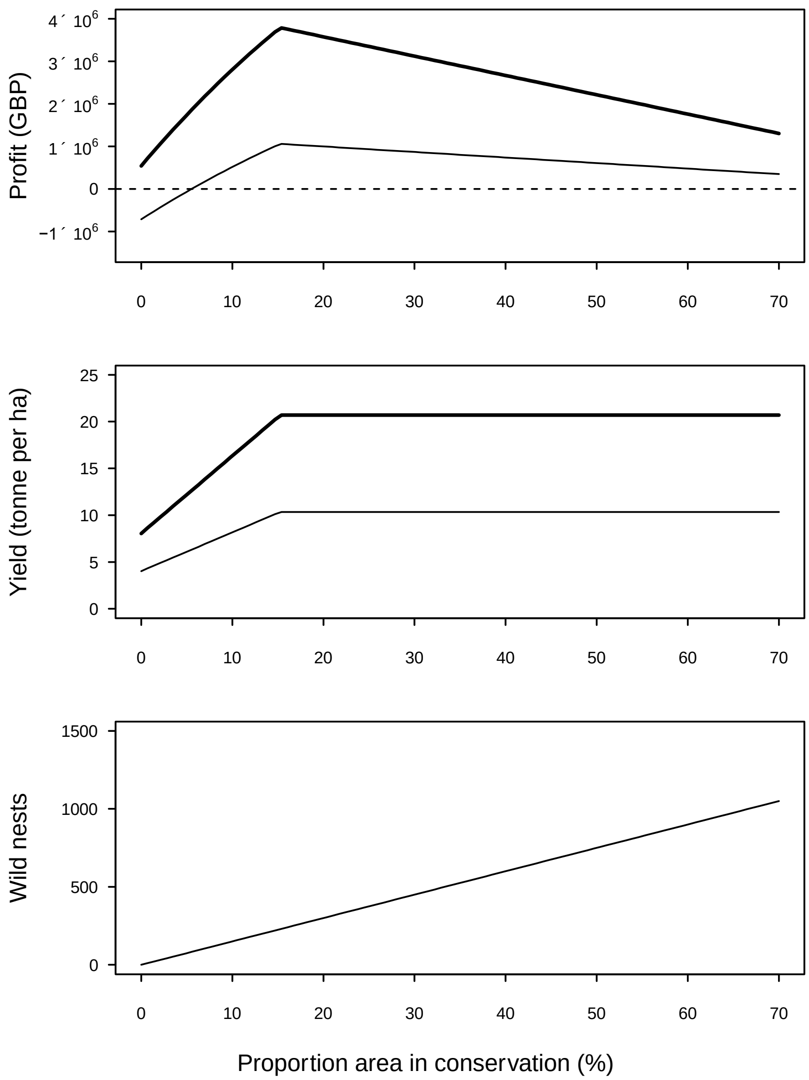

Figure 1: Total profit (a), yield (b), and the number of wild bee nests, N as functions of the proportion of on-farm habitat proportion, v. Thin line: no pesticides; thick line: with pesticides. No commercial bees are used and when pesticides are used, they do not affect wild bees. Parameters as in Table 1.

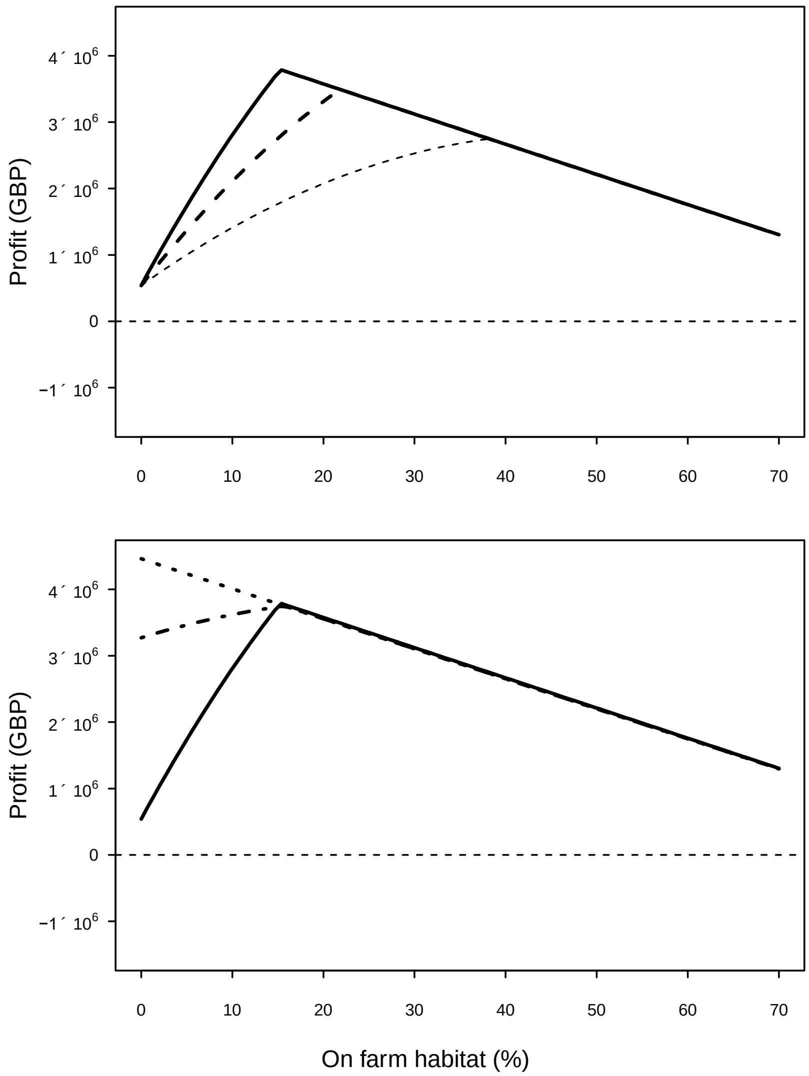

Fig. 2: Total profit as a function of the on-farm habitat proportion, v, for (a) no commercial bees, (b) with commercial bees but with small impact of pesticides, and (c) with commercial bees but with large impact of pesticides. Horizontal line represents zero profit. In (a), solid line corresponds to $w_w = 0$, dashed line to $w_w = 0.3$ and dotted line to $w_w = 0.6$. In (b) dotted line corresponds to no impact of pesticides on wild or commercial bees ($w_w = w_c = 0$), and dash-dot line corresponds to $w_w = w_c = 0.6$ (solid line from (a) is redrawn for comparison). All other parameters as in Table 1.

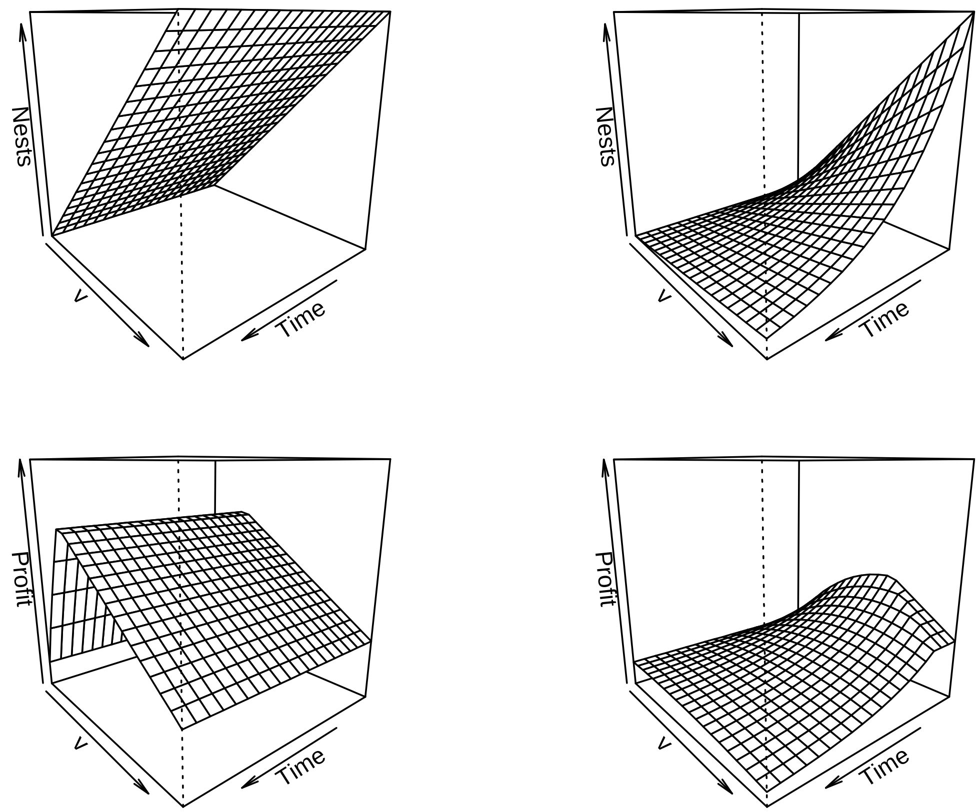

Fig. 3: Dependence of (a) and (b): the number of wild bee nests $N(t)$, and (c) and (d): total profit, on the on-farm habitat proportion, *v* and time (between 0 and 200 years), when pesticides are used but commercial bees are not. In (a) and (c), there is no effect of pesticides on wild bees, $w_w = 0$, and in (b) and (d), $w_w = 0.67$. Other parameters as in Table 1.

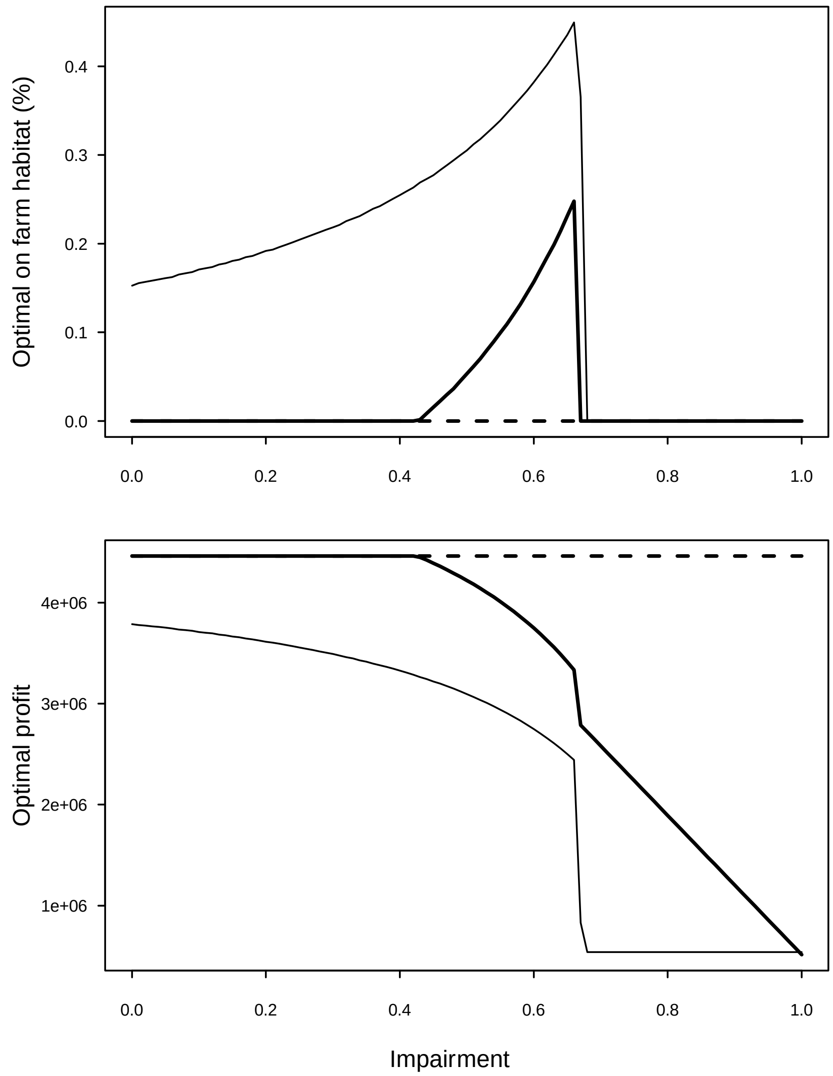

Fig. 4: Dependence of the optimal on-farm habitat proportion (a) and the corresponding total profit (b) on the wild and commercial bee impairment due to pesticides. Thin solid line corresponds to the case without commercial bees; dashed line corresponds to the case with commercial bees, but with no impairment of their performance, $w_c = 0$. For the thick solid line, commercial bees are used and affected by pesticides in the same way as wild bees, $w_c = w_w$. Other parameters as in Table 1.

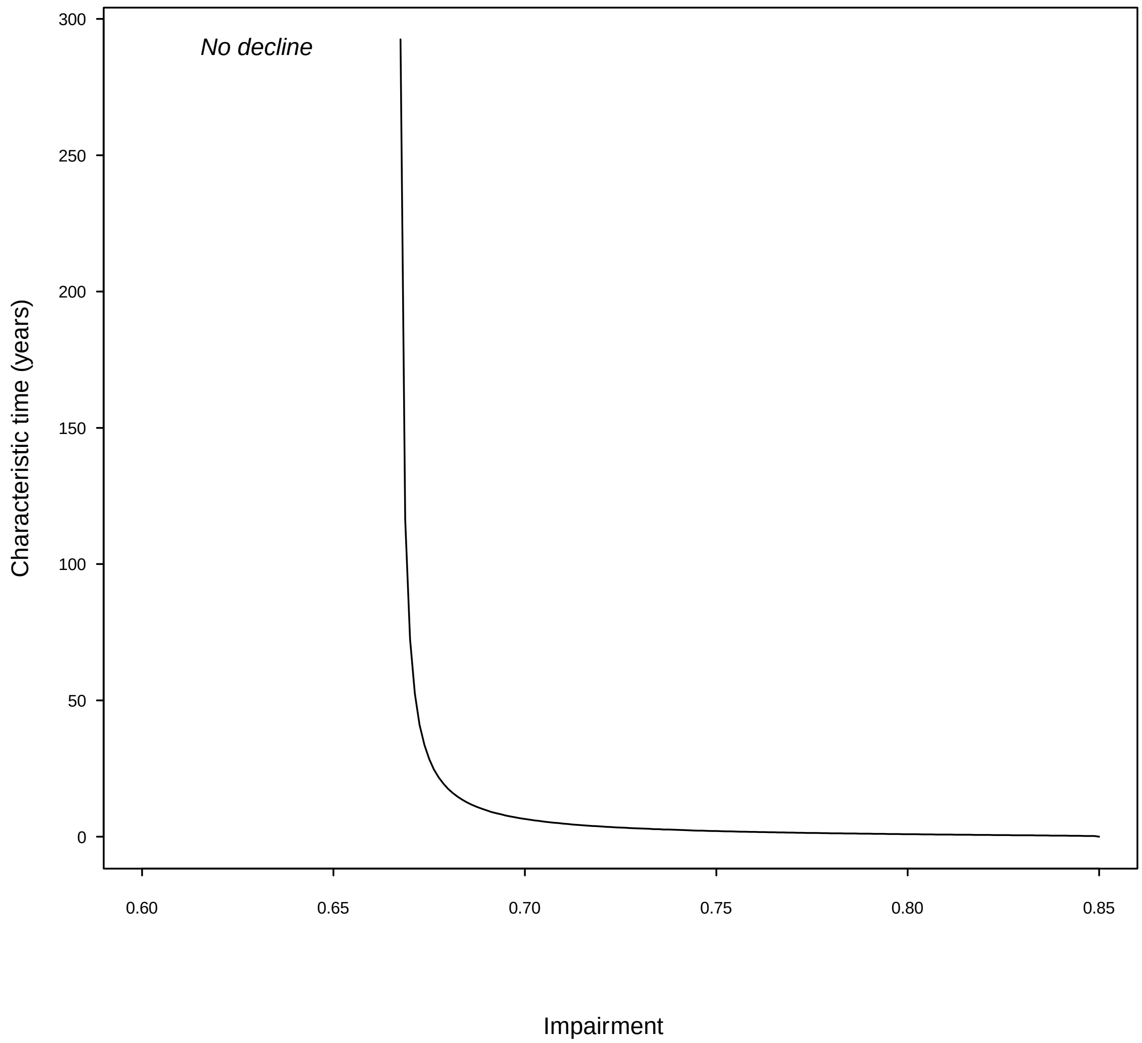

Fig. 5: Dependence of the characteristic time of decay for the wild bee nests, r^{-1} (i.e. time needed for the population to decrease by a factor of e^{-1}, in response to the impairment, w_w.

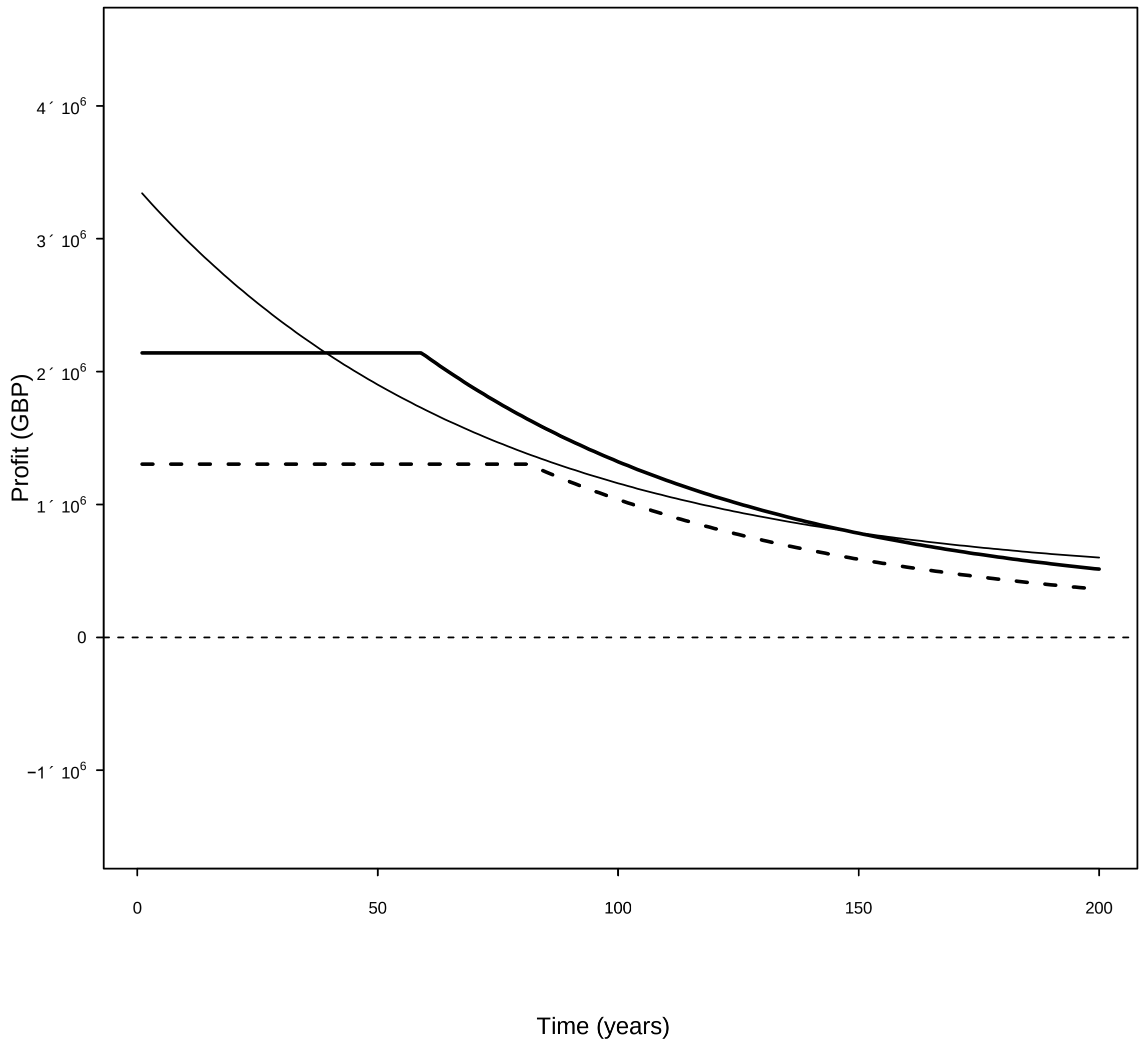

Fig. 6: Examples of time projections for profit over 200 years. Pesticides are used, but no commercial bees; high impact of pesticides on wild bees ($w_w = 0.67$). For illustration, the carrying capacity for wild bees is doubled so that the effect of overpollination is more pronounced. Solid line: *v*=0.22 (optimal), thick line: *v*=0.52, dashed line: *v*=0.7. Other parameters as in Table 1.

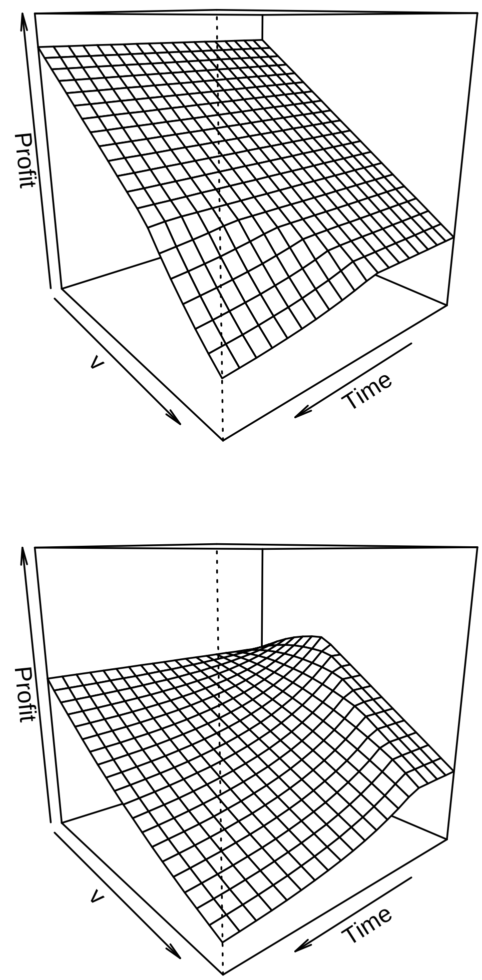

Fig. 7: Comparison of dependence of the profit on time and on-farm habitat proportion for the case when pesticides and commercial bees are used and pesticides strongly affect (a) wild bees only ($w_w = 0.67$, $w_c = 0$) and (b) both wild and commercial bees ($w_w = w_c = 0.67$). Other parameters as in Table 1.

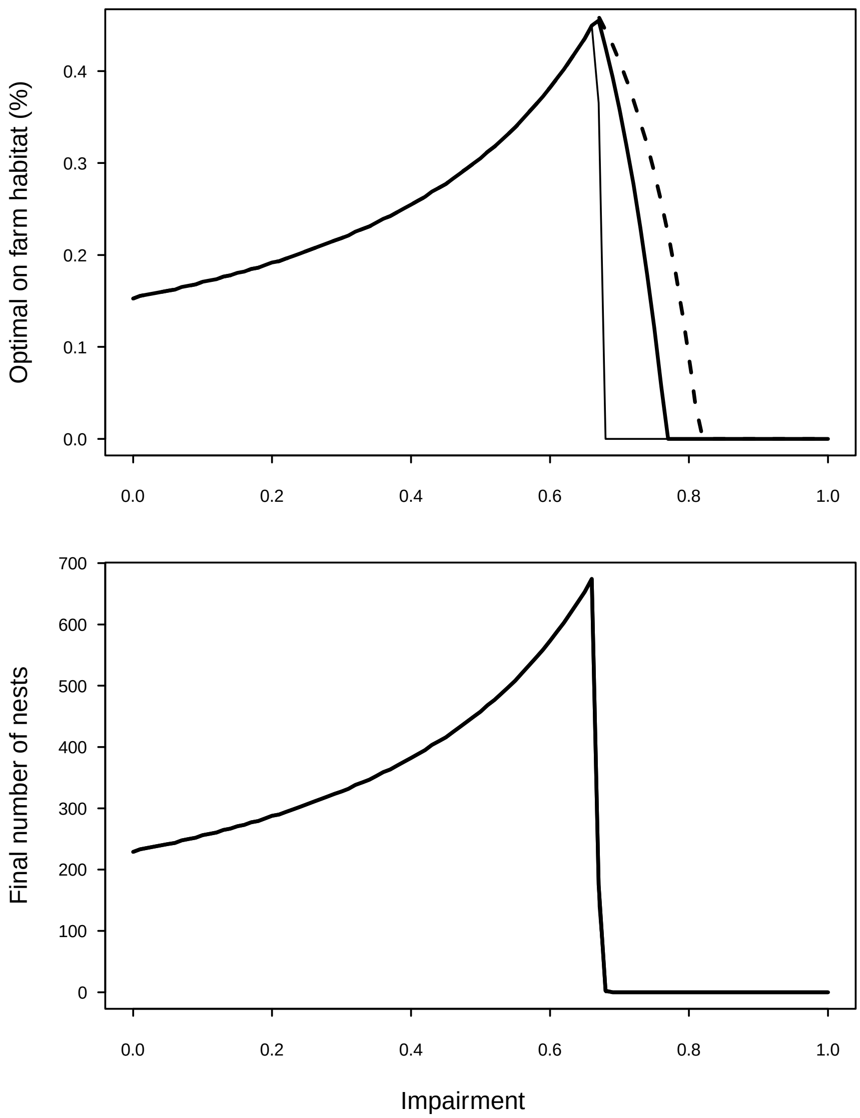

Fig. 8: Dependence of the optimal on-farm habitat proportion (a) and the corresponding long-term number of wild bee nests, $\lim_{t\to\infty} N(t)$, (b), on the wild bee impairment due to pesticides, for different values of the discounting factor, *d*. Thin line: long-term optimal solution, using equation (12); thick line: model with discounting, equation (13), with *d*=0.05; dashed line: equation (13) with *d*=0.1. Only the case with no commercial bees is considered. Other parameters as in Table 1.